

1 **Demographic buffering of life histories?**

2 **Implications of the choice of measurement scale**

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14  
15 Article type: Statistical report

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21 **ABSTRACT**

22 Life-history theory predicts that vital rates that influence population growth the most should  
23 be buffered against environmental fluctuations through selection for reduced variation.  
24 However, it remains unclear whether populations actually are influenced by such  
25 “demographic buffering,” because variation in vital rates can be compared on different  
26 measurement scales, and there has been little attempt to investigate if the choice of scale  
27 influences the chance of detecting demographic buffering. We compared two statistical  
28 approaches to examine whether demographic buffering has influenced vital rates limited  
29 between 0 and 1 in wild Svalbard reindeer. To account for statistical variance constraints on  
30 such vital rates in analyses of demographic buffering, a previously suggested approach is to  
31 scale observed variation with statistical maximum possible variation on the arithmetic scale.  
32 When applying this approach, the results suggested that demographic buffering was  
33 occurring. However, when we applied an alternative approach that identified statistical  
34 variance constraints on the logit scale, there was no evidence for demographic buffering.  
35 Thus, the choice of measurement scale must be carefully considered before one can fully  
36 understand whether demographic buffering influences life histories. Defining the appropriate  
37 scale requires an understanding of the mechanisms through which demographic buffering  
38 may have evolved.

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40 Key words: age structure, demographic buffering, elasticity, integrated population modeling,  
41 life history, matrix modeling, measurement scale, Svalbard reindeer, variance constraints.

42

43 **INTRODUCTION**

44 Several comparative studies indicate that there is a relationship between how influential  
45 fitness components are on population growth and how much they vary over time. More

46 specifically, vital rates whose variation would have a large effect on population growth, as  
47 measured by their sensitivity or elasticity, often show less temporal variation than  
48 components with a lower influence (Pfister 1998, Sæther and Bakke 2000, Gaillard and  
49 Yoccoz 2003, Morris et al. 2011).

50         Models describing stochastic population dynamics suggest that vital rate variation  
51 generally reduces population growth rates (Tuljapurkar and Orzack 1980, Lande et al. 2003).  
52 Tuljapurkar (1982) provided an approximation for the stochastic population growth rate in  
53 age-structured populations which included environmental variances and covariances among  
54 vital rates, as well as the sensitivities of the vital rates. He showed that, not only the  
55 magnitude of variability, but also the impact of the demographic trait on the population  
56 growth rate was important to include when assessing the effects of demographic variation.  
57 Pfister (1998) specifically hypothesized that natural selection should favor a negative  
58 correlation between vital rates' influence on population growth and their variation in order to  
59 minimize variation in population growth rate. Gaillard and Yoccoz (2003) subsequently  
60 suggested that we may expect that influential vital rates would be subject to a canalization  
61 process (environmental canalization) reducing their variance, mediated through selection  
62 against variability. Later studies assessing whether influential vital rates are subject to  
63 selection for low variability have often referred to the term “demographic buffering” (e.g.  
64 Morris and Doak 2004).

65         Evaluation of the demographic buffering hypothesis involves a comparison of the  
66 temporal variation among vital rates that differ in their influence on population growth. If  
67 there is a difference in the level of variation, the question is whether some of that difference  
68 can be explained by natural selection favoring traits that buffer influential vital rates against  
69 fluctuations in the environment. A fundamental methodological challenge is that the  
70 hypothesis is based on population dynamics theory, which raises the question of appropriate

71 scale for comparing temporal variation. For instance, Gaillard and Yoccoz (2003) found that  
72 in long-lived species, in which adult survival is high (often close to 1) and juvenile survival is  
73 lower (e.g.  $\sim 0.5$ ), adult survival was more stable over time and had a larger influence on  
74 population growth compared to juvenile survival. However, they also pointed out that since  
75 survival probability is limited between 0 and 1, its potential variability is related to the mean  
76 survival over time (e.g. if mean survival is close to one, as for adults, large fluctuations over  
77 time are impossible). Thus, vital rates that are bounded by 0 and 1 have a ceiling on the  
78 variance, statistically constraining the temporal variance and the coefficient of variation (CV)  
79 in relation to the mean over time.

80         Because of such variance constraints on many vital rates, it is still not well understood  
81 whether the demographic buffering hypothesis provides a mechanistic explanation for the  
82 empirical pattern that influential fitness components tend to be less variable over time. One  
83 alternative or co-occurring explanation is that vital rates may be subject to directional  
84 selection, possibly resulting in high mean values (Morris and Doak 2004). If this is the case  
85 for influential vital rates limited between 0 and 1, the temporal variation in such vital rates  
86 would be constrained to be low. Accordingly, both theoretical (Morris and Doak 2004) and  
87 empirical (Morris and Doak 2004, Jongejans et al. 2010) studies have suggested that fitness  
88 components with a large influence on population growth may exhibit low temporal variation  
89 without demographic buffering occurring. Thus, the observation that influential fitness  
90 components exhibit little temporal variation is *per se* insufficient to accept the demographic  
91 buffering hypothesis.

92         Gaillard and Yoccoz (2003) and several later studies have attempted to account for the  
93 effects of statistical variance constraints when assessing effects of environmental canalization  
94 or demographic buffering on vital parameters bounded by 0 and 1 in analyses of age-  
95 structured populations. This is, however, challenging. First, age-specific estimates of

96 variances of the vital rate have to be obtained while accounting for observation error and  
97 sampling variance (the latter, for instance in small populations, resulting from demographic  
98 stochasticity). This requires long time series of high quality data and often complex models  
99 that can handle several sources of variability in order to estimate the necessary parameters  
100 (Lande et al. 2003). Second, one must identify the statistical influence of the mean values of  
101 vital rates on their variation pattern, and examine whether demographic buffering has an  
102 effect beyond the effect of statistical constraints.

103         Based on statistical-distribution theory, Morris and Doak (2004) suggested that one  
104 should measure the variance (or CV) of vital rates relative to their statistical maximum  
105 possible variance (referred to as “relativized variance”), and then examine whether influential  
106 rates are less variable relative to this maximum value compared to less influential rates.  
107 Using this approach, studies have indicated that selection for reduced variance in influential  
108 vital rates occurs in some species (e.g. Morris and Doak 2004, Burns et al. 2010, Morris et al.  
109 2011, Rotella et al. 2012), but not that demographic buffering is a universal pattern (Burns et  
110 al. 2010, Jakalaniemi et al. 2013). A challenge with this approach is that the maximum  
111 possible variance of a survival probability would be the variance obtained if the survival  
112 probability in different years is either 0 or 1. This is not an ecologically realistic maximum as  
113 it is unlikely that none, or all individuals, die in a given year. Thus, what is statistically and  
114 ecologically the “maximum possible variance” (or the “maximum possible CV”) is likely to  
115 differ. It is therefore difficult to interpret the biological meaning of “relativized” variances  
116 and how it relates to selection for reduced variance.

117         Given the lack of an underlying evolutionary theory in studies of demographic  
118 buffering, choices of measurement scales for detecting selection for reduced variability are  
119 based on statistical theory. Since temporal variation in vital rates can be compared on a  
120 number of different measurement scales, we examine if the choice of scale affects the

121 interpretation of whether demographic buffering influences vital rates. We develop an  
122 alternative approach to compare temporal variation among vital rates that also handles  
123 statistical variance constraints. We assume that vital rates that are limited between 0 and 1 are  
124 affected by environmental variation similarly across age classes on the logit scale in the  
125 absence of demographic buffering. Given this null-model, the signal from demographic  
126 buffering should be evident in the residual variance, when the common environmental  
127 variance is accounted for. Thus, we can accurately identify the contribution of differences in  
128 mean vital rates to the differences in temporal variation (i.e. the statistical constraint on the  
129 variation of vital rates), without measuring variation relative to theoretical maximum possible  
130 values. This allows us to estimate how much vital rates, with different influences on the  
131 population growth rate, deviate in their temporal variation beyond that expected from  
132 differences in their means. If the deviation in temporal variation is larger than one would  
133 expect from differences in their mean values, the demographic buffering hypothesis would be  
134 supported.

135         We analyze vital rates of a long-lived ungulate, as an example of a group of animals  
136 for which environmental canalization (Gaillard and Yoccoz 2003) or demographic buffering  
137 (Morris et al. 2011) has been suggested to influence the life history. Our analysis is based on  
138 an integrated population model (Kéry and Schaub 2012) that provides age-specific estimates  
139 of vital rates over time while accounting for sampling variance (Lee et al. 2015). We first  
140 apply our approach to examine whether demographic buffering occurs in our population.  
141 Then we apply the previously suggested approach comparing relativized variation among  
142 vital rates that differ in their influence on population growth. Both approaches analyze vital  
143 rates on the arithmetic scale, but they deviate in the scale used for detecting demographic  
144 buffering (logit scale versus “relativized arithmetic scale”). Thus, this will enable us to

145 examine if the choice of measurement scale for detecting demographic buffering affects the  
146 interpretation of whether demographic buffering influences populations.

147

## 148 **METHODS**

149 *Model system.* The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is a high  
150 Arctic wild ungulate endemic to Svalbard, and is characterized by a “slow” life history (cf.  
151 Sæther and Bakke 2000). Data were collected in the Reindalen-Semmeldalen-Colesdalen  
152 valley system (approx. 78N, 16E). The size of our study population (1200 female individuals  
153 on average within the study period) are subject to temporal fluctuations caused by a  
154 combination of winter climate (snow, rain, and ice formation), summer climate (vegetation  
155 growth), and density dependence (Solberg et al. 2001, Stien et al. 2012, Hansen et al. 2013).  
156 Females can give birth to one calf per year. Thus, both survival probability and fecundity are  
157 vital rates bounded by 0 and 1 in our system, which minimizes the chance of “spurious  
158 correlations” resulting from combining vital rates that differ greatly in their statistical  
159 distributions (cf. Morris and Doak 2004, Jakalaniemi et al. 2013).

160 *Model for vital rates.* We estimated female annual survival and fecundity rates by  
161 using a modified version of an integrated population model developed for our study  
162 population of Svalbard reindeer (Lee et al. 2015). This model provides a framework for  
163 estimating age-specific time series of annual survival, fecundity and population sizes, as well  
164 as other population parameters, based on capture-mark-recapture data (CMR, n = 512  
165 individuals) and census data (years 1996-2014). The model incorporates temporal variation in  
166 vital rates (resulting from e.g. fluctuations in population size or environmental stochasticity)  
167 as well as effects of demographic stochasticity. Moreover, the hierarchical model structure,  
168 combining a population process model with an observation model within a Bayesian  
169 framework, allows for uncertain observations and provides uncertainty estimates for all

170 parameters. More details about the modelling framework can be found in Lee et al. (2015)  
 171 and information about additional details relevant for this study is provided in online appendix  
 172 A.

173 The demographic rates were estimated with age-specific means and variance  
 174 components accounting for temporal variation. Such temporal variation can arise because of  
 175 fluctuations in the environment or in population size. In our system, positive correlations  
 176 among age-specific survival rates and among age-specific fecundity rates (Lee et al. 2015)  
 177 indicate that individual responses to such fluctuations are quite similar across age classes.  
 178 Since survival rates and fecundity rates are bounded by 0 and 1 in our population, they were  
 179 modelled as logit-normally distributed variables. The demographic rate  $z$  of an individual in  
 180 age class  $a$  at time  $t$  was then

$$181 \quad \text{logit}(z_{a,t}) = \mu_a^z + \varepsilon_t^z + \gamma_{a,t}^z \quad (1)$$

182 where  $\mu_a^z$  is the mean for age class  $a$ . The first variance component ( $\varepsilon_t^z$ ) accounts for  
 183 synchronous fluctuations in the demographic rate among age classes over time. The second  
 184 variance component ( $\gamma_{a,t}^z$ ) is a residual term accounting for age-specific deviations from the  
 185 common temporal fluctuations. It was assumed that  $\varepsilon_t^z \square N(0, \sigma_{\varepsilon(z)}^2)$  and  $\gamma_{a,t}^z \sim N(0, \sigma_{\gamma(z)}^2)$ .

186 If  $\gamma_{a,t}^z = 0$  it means that temporal fluctuations in a type of vital rate  $z$  are equal among  
 187 the age classes on the logit scale. On the arithmetic scale, however, fluctuations are  
 188 synchronous among age classes but the magnitude varies when  $\mu_a^z$  differs among age classes.  
 189 Since the coefficient of variation on the arithmetic scale ( $\text{CV} = \text{standard deviation}/\text{mean}$ )  
 190 decreases with increasing mean for logit-normally distributed variables, age classes with the  
 191 lowest mean of  $z$  will exhibit proportionally larger fluctuations in  $z$  (measured by the CV of  $z$   
 192 on the arithmetic scale). As long as  $\gamma_{a,t}^z = 0$ , these age-differences in the CV of  $z$  are purely a  
 193 result of different means among the age classes, provided that our model (eq. 1) is



194 appropriate (i.e. the “statistical” effect). In contrast, if  $\gamma_{a,t}^z \neq 0$ , the differences in the CV of  $z$   
195 among age classes are different from those expected based purely on age-differences in the  
196 mean of  $z$ . Thus, this situation could allow demographic buffering to occur.

197         The integrated population model was fitted to the data in a Bayesian framework using  
198 MCMC techniques (Kéry and Schaub 2012). Thus, all estimates of vital rates and associated  
199 parameters were represented by a joint posterior distribution (more details about model  
200 implementation can be found in online appendix A). The following analyses were performed  
201 for each sample of the posterior distribution so that all resulting estimates were associated  
202 with an uncertainty estimate (i.e. 95% credible intervals (CrI)).

203         *Influence of vital rates.* The elasticity of the deterministic growth rate to changes in  
204 the mean of vital rates are often negatively related to the CV of vital rates in analyses of  
205 demographic buffering (e.g. Pfister 1998, Morris and Doak 2004, Jongejans et al. 2010). We  
206 therefore conducted an elasticity analysis to estimate the influence of each rate on the  
207 population growth rate in our study population (Caswell 2001). Based on the estimates of  
208 annual vital rates on the arithmetic scale provided by the integrated population model, we  
209 constructed an average projection matrix parameterized according to a post breeding census  
210 (Caswell 2001). This was done for each sample of the joint posterior distribution of vital rates  
211 (for details see online appendix B). The elasticity ( $E$ ) of  $\lambda$  to the vital rate  $z$  was then  
212 estimated as the proportional change in  $\lambda$  resulting from a proportional change in the mean of  
213 vital rate  $z$  on the arithmetic scale (Caswell 2001). Since the dimension of the projection  
214 matrix influences estimates of elasticities (e.g. by how population structure is defined, Pfister  
215 1998), we performed the analysis for complete age structure as well as for the aggregated age  
216 classes for which the vital rates originally were estimated (see online appendix B for the  
217 different projection matrices).

218           *Relation between temporal variation and influence of vital rates.* The temporal  
219 variation of a vital rate was estimated as the CV of annual estimates of the vital rate on the  
220 arithmetic scale. Based on the matrix model with full age structure we performed linear  
221 regressions between  $\ln(E)$  and CV for survival rates (A) and fecundity rates (B) separately, in  
222 addition to a pooled analysis with all rates (C). Based on the aggregated age classes we  
223 performed one regression with survival and fecundity rates combined (D), since separate  
224 analyses for survival and fecundity would include only 6 and 5 vital rates each. The analyses  
225 were carried out for each sample of the posterior distribution. This provided a total of 9090  
226 samples of the regression coefficients. If the CrI of the estimated regression slopes did not  
227 span zero, we considered a relationship between  $\ln(E)$  and CV to be present.

228           *Examining the demographic buffering hypothesis.* We expected the CV of vital rates  
229 to be negatively related to  $\ln(E)$ . This is because elasticity generally increases whereas CV  
230 decreases with the mean of a vital rate bounded by 0 and 1 (Morris and Doak 2004). To  
231 assess whether demographic buffering may have additionally contributed to this negative  
232 relationship, we examined whether differences in the magnitude of temporal variation among  
233 more or less influential vital rates were larger than we would expect from the differences in  
234 their means given our model (eq. 1). We therefore carried out a second elasticity and  
235 regression analysis with a new set of vital rates simulated from the previous estimates of  
236 survival and fecundity. In these simulations, the variance components accounting for  
237 deviations from common fluctuations among age classes were set to zero (i.e.  $\gamma_{a,t}^z = 0$ ). Thus,  
238 age-differences in temporal variation on the arithmetic scale were solely a result of the age-  
239 differences in the mean of vital rates (mimicking the absence of demographic buffering). In  
240 the presence of demographic buffering, we would expect the slope of the observed  
241 relationship between CV and  $\ln(E)$  to be steeper than that obtained from the simulated data.  
242 In contrast, if the observed and simulated relationships were equal, it would indicate that

243 demographic buffering is not needed to explain the negative relationship between the  
244 influence of vital rates and their temporal variation.

245 Finally, we examined whether we would reach the same conclusion using relativized  
246 CV as the scale for comparing temporal variation among vital rates following suggestions of  
247 Morris and Doak (2004). Thus, we tested the demographic buffering hypothesis as if we only  
248 had point estimates of vital rates (i.e. the means of posterior distributions provided by the  
249 integrated population model), disregarding the estimate uncertainty and the information of the  
250 underlying process of vital rates. For the four combinations of vital rates described above (A-  
251 D) the “relativized” CV was related to the elasticity of vital rates using Spearman’s  
252 correlation analyses (Pfister 1998, Morris and Doak 2004). The correlation coefficients ( $r$ )  
253 were estimated with significance levels calculated for one-tail test of the hypothesis  $r < 0$ .

254

## 255 RESULTS

256 The estimated mean annual survival was largest for 1 and 2-year-olds, followed by 3-8-year-  
257 olds (Table 1). Calves, 9-11-year-olds, and individuals of 12 years and older had significantly  
258 lower mean survival. The estimated mean fecundity (only including female offspring) was  
259 highest for 4-9-year-olds, whereas the lowest offspring production was found among 2-year-  
260 olds followed by individuals older than 12 years (Table 1). Temporal fluctuations in survival  
261 and fecundity were highly correlated among age classes (online appendix C). Thus the  
262 contribution from the common variance component to the total variance in each of the vital  
263 rates was large compared to the residual variance (annual survival,  $\sigma_{\varepsilon(\text{survival})} = 1.86$  (CrI 1.21,  
264 2.84) vs.  $\sigma_{\gamma(\text{survival})} = 0.45$  (0.06, 0.93); fecundity (including female and male offspring),  
265  $\sigma_{\varepsilon(\text{fecundity})} = 1.08$  (0.75, 1.56) vs.  $\sigma_{\gamma(\text{fecundity})} = 0.25$  (0.01, 0.56)). On the arithmetic scale,  
266 fecundity rates were proportionally more variable than survival rates (shown by larger CVs,  
267 Table 1). In addition, the age classes with lower annual survival and fecundity (younger and

268 older individuals) exhibited proportionally larger fluctuations over time than age classes with  
269 higher annual survival and fecundity (prime-aged individuals).

270 The estimated elasticities were in general larger for survival rates than for fecundity  
271 rates (Table 1). Moreover, prime-aged individuals had the largest  $E$  within each of the two  
272 types of vital rates. Relatively large estimates of  $E$  were also obtained for the mean annual  
273 survival of calves, yearlings, and two year-olds. The two oldest age classes (9-11, and 12+)  
274 had smaller influence on population growth than younger age classes.

275 There was a negative relationship between CV and  $\ln(E)$  of vital rates, indicating that  
276 vital rates with a large influence on population growth were less variable than vital rates with  
277 smaller influence (Fig. 1). This was true irrespective of matrix dimension and whether or not  
278 survival and fecundity rates were pooled. The simulated relationships in which demographic  
279 buffering was absent were not statistically different from the observed relationships, as  
280 indicated by overlapping CrIs for observed and simulated slopes (Fig. 1). This was due to the  
281 large estimate of the common variance components ( $\varepsilon_i^z$ ) compared to the residual  
282 components ( $\gamma_{a,t}^z$ ). Thus, demographic buffering was not required to explain the observed  
283 negative relationships between CV and  $\ln(E)$ .

284 Finally we checked whether we would obtain the same conclusions using Spearman's  
285 correlations between  $E$  and temporal variation of vital rates measured by relativized CV.  
286 There were significant negative correlations in the three analyses including full age structure  
287 (A-C,  $r = -0.57, -0.61, \text{ and } -0.66$  respectively, all p-values  $< 0.003$ ). The correlation with  
288 aggregated age classes was also negative but not significant (D,  $r = -.22, \text{ p-value} = 0.25$ ).  
289 Thus, using relativized CV as a measure of variation gave some support for the demographic  
290 buffering hypothesis.

291

292 **DISCUSSION**

293 We found no evidence of demographic buffering of the vital rates with the largest influence  
294 on population growth when we identified their variance constraints on the logit scale. Vital  
295 rates with greater elasticity did indeed exhibit lower temporal variation than vital rates with  
296 smaller elasticity. However, using detailed information about the underlying process of the  
297 vital rates measured on the logit scale, we found that the deviations in temporal variation  
298 among more or less influential vital rates were not larger than we would expect from their  
299 different means. This indicates that demographic buffering did not contribute to the temporal  
300 stability of influential vital rates in the Svalbard reindeer. If we did not have the same amount  
301 of information about the pattern of variation of the vital rates, the opposite conclusion could  
302 have been made based on commonly applied methods (i.e. by scaling the observed temporal  
303 variation by the statistical maximum variation). It is already recognized that estimates of  
304 elasticity and its relationship with temporal variation hinge on the methodology used (Morris  
305 and Doak 2004). Here, the key difference between the two methods, yielding contrasting  
306 conclusions, is how the mean and the variance of vital rates are assumed to be related in the  
307 absence of demographic buffering. Both approaches can be reasonable argued for, indicating  
308 that we need to better understand the underlying mechanisms, through which demographic  
309 buffering may have evolved, to define a meaningful measurement scale.

310 Survival of prime-aged individuals (3-8 years) had a large influence on population  
311 growth and exhibited little temporal variation compared to fecundity and juvenile survival in  
312 the Svalbard reindeer. This confirms previous patterns found in long-lived organisms  
313 (Gaillard et al. 2000, Sæther and Bakke 2000, Gaillard and Yoccoz 2003). However,  
314 identifying variance constraints on the logit scale generated results that contradict previous  
315 studies on ungulates suggesting that these patterns cannot be fully explained by the high  
316 mean value of adult survival (Gaillard and Yoccoz 2003, Morris et al. 2011). This contrasting  
317 result could be caused by natural selection favoring a high mean survival of prime-aged

318 individuals in this species, which can only occur if temporal variation in annual survival is  
319 low. Still, there was no evidence of selection against variability in adult survival given our  
320 model.

321         The age-specific means of vital rates influence both the temporal variation of vital  
322 rates and the elasticities (or sensitivities) of vital rates through the stable age structure and  
323 reproductive values. Negative correlations between variability and influence of vital rates on  
324 population growth rates in comparative studies may consequently arise simply because of  
325 interspecific life-history variation reflected by tradeoffs between survival and reproduction  
326 (cf. Sæther and Bakke 2000, Gaillard and Yoccoz 2003).

327         In the Svalbard reindeer, major population declines have occurred following winters  
328 with large population size and ice covering the feeding grounds, causing increased  
329 competition for food (Solberg et al. 2001, Stien et al. 2012). These declines are associated  
330 with low reproductive rates in all age classes, leading to relatively large temporal variation in  
331 fecundity, whereas survival of prime-aged individuals remains high (our study; Lee et al.  
332 2015). At the same time, the high mean survival of prime-aged individuals combined with  
333 lower mean survival of calves and low mean fecundity in the population, result in an age  
334 structure with a large proportion of adult individuals with high reproductive value (results on  
335 estimated age structure and reproductive values of Svalbard reindeer can be found in online  
336 appendix D). Thus, this life-history pattern generates high elasticity of survival of prime-aged  
337 individuals (which has low variability) and lower elasticity of fecundity and calf survival  
338 rates (which have higher variability) (cf. Gaillard et al. 2000, Sæther and Bakke 2000,  
339 Gaillard and Yoccoz 2003, Oli 2004).

340         Survival seems to be protected against effects of variation in environmental conditions  
341 by reduced fecundity when resources are limited, leaving opportunities for reproduction in  
342 later years. This is described, in the environmental canalization hypothesis, as a risk avoiding

343 tactic reducing variability of influential vital rates (Gaillard and Yoccoz 2003). Thus, our  
344 study supports some of the demographic processes previously suggested to cause observed  
345 patterns of variation in vital rates, but still reveals challenges in approaching the underlying  
346 evolutionary mechanisms.

347         In order to understand how demographic buffering may contribute to shaping life  
348 histories we need to better understand evolutionary processes reducing temporal variation in  
349 influential vital parameters. There are many traits that affect the means and variances of vital  
350 rates, and there are likely some tradeoffs in those traits. For instance, low variability in adult  
351 survival and higher variability in juvenile survival found in ungulates (Gaillard et al. 1998)  
352 may be explained by tradeoffs in energy allocation to offspring investment and to the  
353 probability of own survival. A precise formulation of such tradeoffs, including the interaction  
354 between ecological and evolutionary processes, is required to obtain meaningful  
355 measurements of demographic buffering (cf. Boyce et al. 2006, Houle et al. 2011). Our study  
356 indicates that how we measure reduction in variation is of great importance in ecological  
357 interpretations of demographic buffering based on analyses of population dynamics.

358

### 359 *Acknowledgments*

360 This study was financed by The Research Council of Norway (RCN) (SFF-III, project  
361 223257) as well as the programs NORKLIMA (project 178561/S30) and POLARPROG  
362 (project 216051). We are grateful to Christophe Pélabon, Justin Irvine, Erik Ropstad, Vebjørn  
363 Veiberg, Rolf Langvatn, Odd Halvorsen, and students and staff at The University Centre in  
364 Svalbard (UNIS) for contributions to the study. We also thank J.M. Gaillard and one  
365 anonymous reviewer for constructive comments improving the manuscript. Data collection  
366 was mainly financed by RCN, UK Natural Environment Research Council, and the Macaulay  
367 Development Trust.

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428

429

430 Table 1. Estimates of annual survival and fecundity of Svalbard reindeer.

Age	Mean	CV	<i>E</i>
Survival			
0	0.80 (0.75, 0.84)	0.28 (0.24, 0.32)	0.14 (0.14, 0.15)
1	0.99 (0.97, 1.00)	0.02 (0.00, 0.04)	0.14 (0.14, 0.15)
2	0.99 (0.99, 1.00)	0.01 (0.00, 0.02)	0.14 (0.13, 0.14)
3-8	0.98 (0.97, 0.99)	0.03 (0.02, 0.04)	0.50 (0.49, 0.52)
9-11	0.89 (0.85, 0.92)	0.16 (0.10, 0.21)	0.06 (0.05, 0.06)
12+	0.74 (0.67, 0.79)	0.31 (0.25, 0.38)	0.01 (0.01, 0.02)
Fecundity			
2	0.07 (0.05, 0.10)	0.62 (0.52, 0.79)	0.01 (0.00, 0.01)
3	0.27 (0.24, 0.30)	0.39 (0.33, 0.45)	0.02 (0.02, 0.02)
4-9	0.32 (0.31, 0.33)	0.33 (0.30, 0.35)	0.09 (0.09, 0.10)
10-12	0.29 (0.25, 0.32)	0.36 (0.31, 0.42)	0.02 (0.02, 0.02)
13+	0.17 (0.11, 0.22)	0.52 (0.42, 0.68)	0.01 (0.00, 0.01)

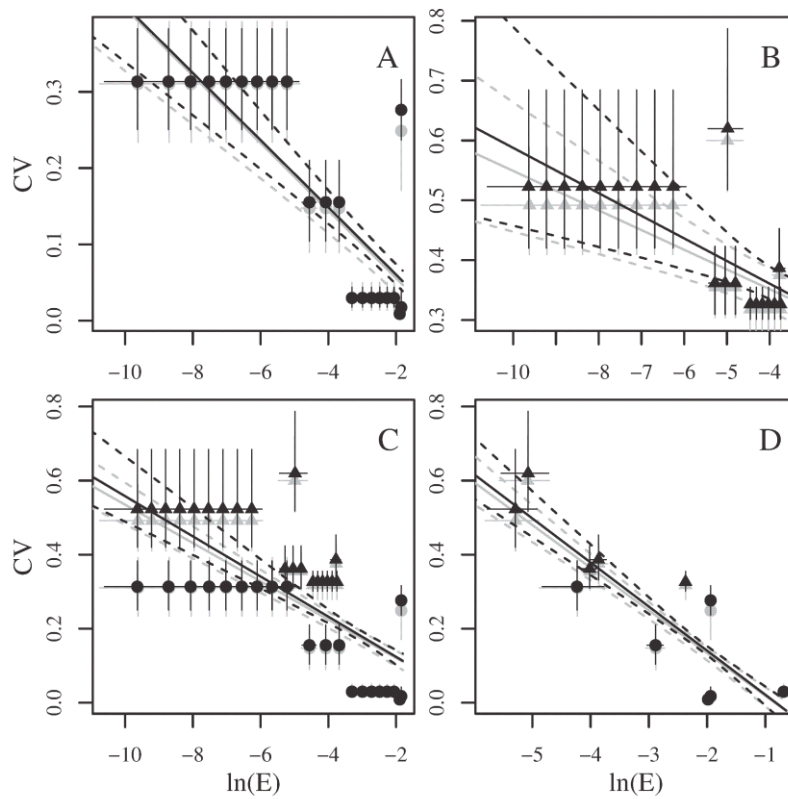
431

432 Note: Mean and CV of survival is estimated for 1996-2013. Mean and CV of fecundity is  
 433 estimated for 1997-2014 and includes only female offspring. The deterministic population  
 434 growth rate's elasticity (*E*) with respect to the mean survival and fecundity rates are estimated  
 435 from the average projection matrix. Uncertainties of estimates are represented by the 95%  
 436 credible interval (parenthesis).

437 **FIGURE LEGENDS**

438

439 Fig. 1. Relationships between the influence of vital rates on population growth rate ( $\ln(E)$ )  
440 and their temporal variation (CV). The observed relationships (black solid lines) are not  
441 significantly different from simulated regressions in which demographic buffering is absent  
442 (grey solid lines). The uncertainty (95% CrI) in regression lines is displayed with dashed  
443 lines. Points (survival rates) and triangles (fecundity rates) are the means of posterior  
444 distributions of estimated (black) and simulated (grey) vital rates. The uncertainties (95%  
445 CrI) in the estimates are displayed with vertical and horizontal lines. Observed relationships:  
446 A) Only survival rates with full age structure, slope = -0.044 (-0.053, -0.035),  $R^2 = 0.67$   
447 (0.58, 0.74),  $n = 21$ . B) Only fecundity rates with full age structure, slope = -0.038 (-0.070, -  
448 0.017),  $R^2 = 0.54$  (0.21, 0.77),  $n = 20$ . C) Survival and fecundity rates combined with full age  
449 structure, slope = -0.054 (CrI -0.070, -0.045),  $R^2 = 0.52$  (0.43, 0.61),  $n = 41$ . D) Survival and  
450 fecundity rates combined with aggregated age classes, slope = -0.12 (-0.14, -0.10),  $R^2 = 0.74$   
451 (0.69, 0.79),  $n = 11$ . Simulated relationships: A) Slope = -0.052 (CrI -0.060, -0.045),  $R^2 =$   
452 0.52 (0.44, 0.61). B) Slope = -0.033 (-0.051, -0.017),  $R^2 = 0.52$  (0.25, 0.70). C) Slope = -  
453 0.044 (-0.054, -0.035),  $R^2 = 0.70$  (0.60, 0.78). D) Slope = -0.12 (-0.13, -0.10),  $R^2 = 0.75$   
454 (0.71, 0.79).



455

456 Fig. 1. Relationships between the influence of vital rates on population growth rate ( $\ln(E)$ )  
 457 and their temporal variation (CV). The observed relationships (black solid lines) are not  
 458 significantly different from simulated regressions in which demographic buffering is absent  
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 470  $0.044$  ( $-0.054, -0.035$ ),  $R^2 = 0.70$  ( $0.60, 0.78$ ). D) Slope =  $-0.12$  ( $-0.13, -0.10$ ),  $R^2 = 0.75$   
 471 ( $0.71, 0.79$ ).